

Opinion

Forecasting species' responses to climate change using space-for-time substitution

Heather M. Kharouba ^{1,*} and Jennifer L. Williams²

To anticipate species' responses to climate change, ecologists have largely relied on the space-for-time-substitution (SFTS) approach. However, the hypothesis and its underlying assumptions have been poorly tested. Here, we detail how the efficacy of using the SFTS approach to predict future locations will depend on species' traits, the ecological context, and whether the species is declining or introduced. We argue that the SFTS approach will be least predictive in the contexts where we most need it to be: forecasting the expansion of the range of introduced species and the recovery of threatened species. We highlight how evaluating the underlying assumptions, along with improved methods, will rapidly advance our understanding of the applicability of the SFTS approach, particularly in the context of modelling the distribution of species.

A ubiquitous yet poorly tested hypothesis with consequential impacts

In an epoch of rapid environmental change, scientists are increasingly being asked to **predict** (see [Glossary](#)) the impact of these changes on biodiversity. Since we seldom have sufficient historical long-term data to predict the future, spatial species–climate associations are often used as a proxy to **forecast** biotic responses to climate change, known as the **space-for-time-substitution (SFTS) approach**. For example, elevational variations in temperature have been used to predict how climate change will affect biodiversity along the gradient (e.g., [1]). This approach is based on the **SFTS hypothesis** that the biotic–climate relationships observed over space are causal. The SFTS approach has been applied to multiple biotic responses (e.g., abundance, occupancy, richness [1–3]) and harnessed by **species distribution models (SDM)**, also called ecological niche models. SDMs correlate species' occurrence records with georeferenced environmental data, and **project** these relationships to future climate conditions to predict how species will shift their ranges in response to climate change [4,5].

Despite being ubiquitous in ecology, the SFTS hypothesis has seldom been tested. When it has been, there has been mixed support [6]. Some studies have urged caution when predicting changes in abundance [7] or **predictions** over longer timescales [8], whereas others have found moderate support [9,10] or that it works well [11,12]. Previous research has largely focused on whether the approach works in a specific case such as a particular taxonomic group such as birds (i.e., results-focused research) rather than testing why or when it should be **predictable** (i.e., identifying the underlying mechanisms; but see [13]). Despite these efforts, we still have no substantive ability to decipher the degree of uncertainty associated with predictions generated by the SFTS approach. Given the urgency of **anticipating** responses to climate change and that experiments are time-consuming, it is critical to leverage the existing data more effectively.

Here, we focus on biological hypotheses that are relevant to predicting where a species will be in the future with climate change, and on species–climate relationships formed by *in situ* spatial

Highlights

Forecasting species' responses to climate change is critical and challenging.

One commonly used approach is space-for-time substitution (SFTS), which takes the hypothesis that the biotic–climate relationships observed over space are causal, and uses this spatial relationship to predict responses over time.

The underlying assumptions have seldom been tested; if not supported, the resulting predictions can be biased and have a high degree of uncertainty.

We currently cannot discern for which type of species the SFTS approach is likely to be more reliable.

We argue that the way forward is to test the underlying assumptions by evaluating contexts and species using a comparative approach, through improvements in the quality of biological data, and through the integration of experimental and modelling approaches to the distribution of species.

¹Department of Biology, University of Ottawa, Ontario, ON, K1N 6N5, Canada

²Department of Geography and Biodiversity Research Centre, University of British Columbia, Vancouver, BC, V6T 1Z2, Canada

*Correspondence:
heather.kharouba@uottawa.ca
(H.M. Kharouba).

climate gradients in terrestrial systems. We use changes in temperature as a proxy for climate change and, for simplicity, did not consider habitat modifications. Additionally, we realize that future climate conditions could be different from the current ones for many reasons (e.g., [12,14]).

Overview of the SFTS hypothesis

The SFTS hypothesis makes several biological assumptions related to forecasting. Here, we focus on four:

1. **Climate determinism.** Climate is the primary determinant of biotic responses (fitness). For example, if temperature is the primary determinant, underlying the SFTS hypothesis is a theoretical **thermal performance curve (TPC)** (Box 1). If this assumption is not met, we will be unable to accurately predict changes in fitness on the basis of climate change.
2. **Climate equilibrium.** Species occur in all locations where the climate is favourable and are absent where the climate is not. If this assumption is not met, we are unlikely to accurately predict potential suitable conditions and future locations.
3. **Climate conservatism.** Species' niches change very slowly over timescales that are relevant to ecological predictions, so species will continue to occupy similar environmental conditions in the future. Alternatively, if the niches shift over time, then the current climate conditions associated with species' suitability will not be **predictive** of future favourable conditions.
4. **Climate spatial conservatism.** A species-level niche is the same as that of individual populations. If not – that is, if niches differ over space (e.g., if the populations are locally adapted) – then species-level climatic tolerance inferred across space might not be a good predictor of the response of any single population.

Box 1. Illustrating the space-for-time substitution (SFTS) approach and predicting where a species will be under climate change

According to first principles, species should follow a theoretical thermal performance curve (TPC) (Figure 1A). Here, we use temperature change as a proxy for climate change and give an example for three scenarios of how species' ranges could respond to climatic warming. For simplicity, we do not consider potential interactions between the assumptions.

Scenario 1: Dispersal ability (Figure 1C): We assume both species have reached equilibrium under the current climate, but future spatial predictions diverge at poleward latitudes depending on their ability to disperse. Under future climate, suitability decreases in the warmest locations regardless of the dispersal ability (the habitat's suitability in Figure 1B is the same for both species). A strong disperser would track with the suitable climate at the poleward latitudes, but a weak disperser would (i) lag behind the suitable climate at the poleward edge, thus underestimating the total range size in the future (i.e., a smaller range size than the strong disperser) for the weak disperser; and (ii) have greater uncertainty in the predictions of the future range. Predictions for contraction of the range at the southern limit where temperatures become too hot are similar for both species.

Scenario 2: Introduced species in their native vs. introduced range (Figure 1D). We illustrate one scenario and assume the introduced species has limited dispersal in its introduced range. We predict that the current distribution of the introduced range is not at climate equilibrium and therefore it has a smaller total current range size than the native range due to the suitability–temperature relationship (Figure 1B). As a result, predictions of the future introduced range will underestimate the total range size (i.e., a smaller range size than the native range). We also predict greater uncertainty in the future introduced range.

Scenario 3: Species with different interaction strengths (Figure 1E). We illustrate one spatial prediction comparing species that are strong or weak interactors (and do not necessarily interact with each other). We assume that both species have reached equilibrium under the current climate, and predict that the weak interactor will track with the shift in the suitable future climate. The prediction for the strong interactor is based solely on a positive interaction (i.e., facilitation). We predict that the strong interactor occurs at higher latitudes in its current range than the weak interactor (the larger purple area), given facilitation, but because of its weaker relationship with climate than the weak interactor (Figure 1B), it would lag behind a suitable climate (no red area at poleward range). Further, we have far more uncertainty about this prediction than in other scenarios – and at both edges of the range – because the prediction is dependent on the response of multiple species to warming, as well as the strength and type of their interaction.

Glossary

Anticipate: a weaker form of prediction, with higher uncertainty than a prediction.

Climate decoupling: a quantitative estimate of how species' occurrence (abundance and distributions) are related to nonclimatic factors more than to climatic factors (i.e., more decoupling equals less accurate predictions).

Climate matching: the extent to which species' abundance and distributions are predicted by climate (i.e., worse matching equals less accurate predictions).

Forecast: the act of making a prediction about the future using data from the past or present.

Predictable: a state or outcome that is capable of being predicted. With sufficient understanding of the system, the prediction would be precise and accurate.

Prediction: a formal statement about a future event or outcome.

Predictive: the ability of the observed outcome to match the expected outcome.

Projection: a prediction about what would happen, given certain hypotheses, conditions, or assumptions.

Space-for-time substitution (SFTS) approach: this relies on the SFTS hypothesis to predict species' responses in time based on biotic–climate relationships across a spatial gradient. This approach has been applied to multiple biotic responses (e.g., abundance, distribution, and richness).

Space-for-time substitution (SFTS) hypothesis: the hypothesis that the biotic–climate relationships observed over space are causal.

Species distribution model (SDM): a spatial prediction of a species' suitable habitat based on correlations between georeferenced occurrence records and a set of environmental variables with geospatial data.

Theoretical thermal performance curve (TPC): a causal relationship, where a species' performance is bounded between lower and upper critical limits and is at the maximum at the species' optimal temperature.

Transferability: a dimension of a model's performance, or the degree to which a model built in one place or time can successfully predict distributions in a different place or time (i.e., lower transferability equals less accurate predictions).

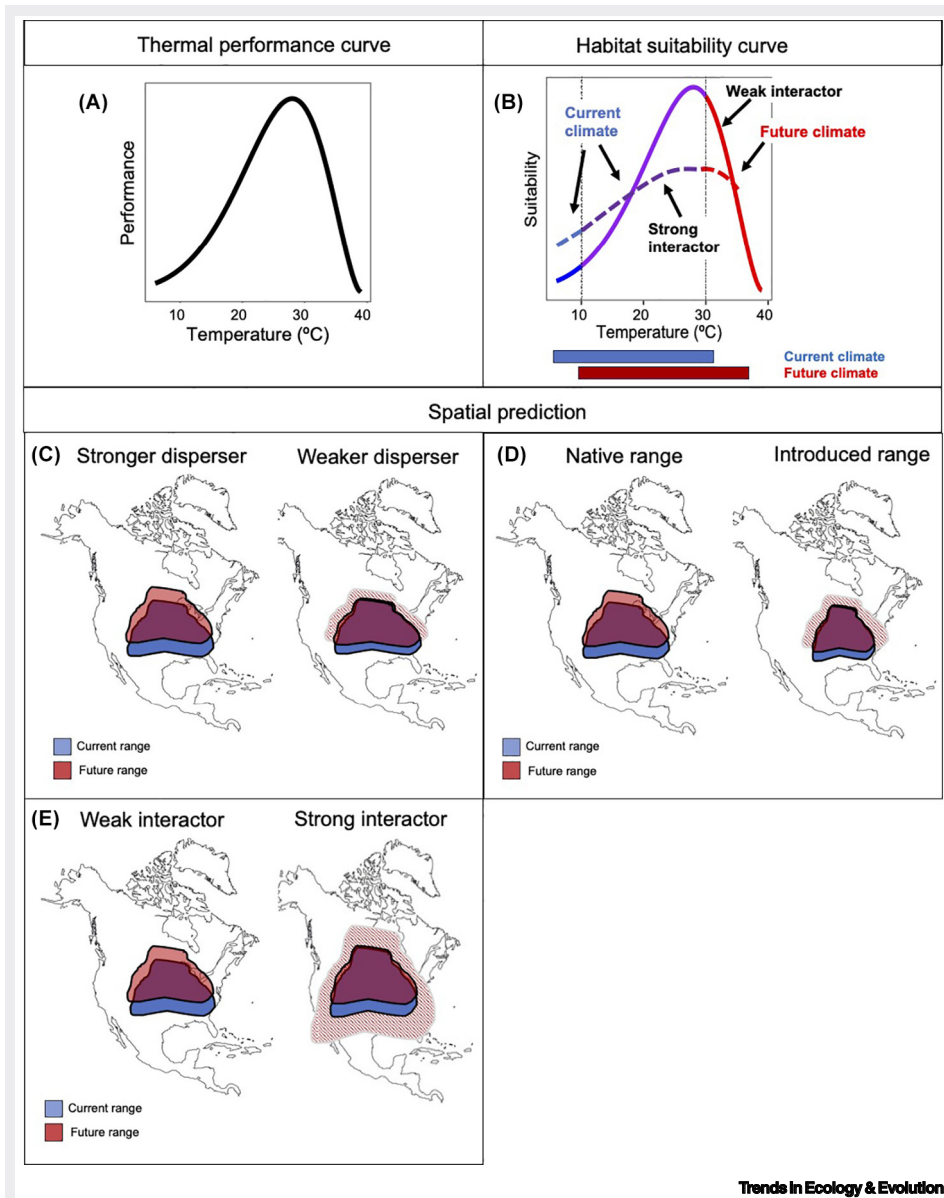


Figure 1. A comparative framework for testing the SFTS hypothesis. (A) First principles. Theoretical thermal performance curve (TPC). (B) Relationship between the habitat's suitability and temperature under the current and future climate, based on the TPC. We assume that performance scales linearly with suitability. The relationship is likely to be independent of dispersal and the species' origin but dependent on the interaction's strength. For strongly interacting species (dashed line), the relationship between suitability and temperature is weaker than that of the weak interactors (solid line). Vertical lines highlight shifts in temperature (as the temperature warms across all locations, the line on the left represents the lowest temperature under the future climate, and the line on the right is the highest temperature under the current climate). (C–E) Three scenarios for spatial predictions based on the relationship between the habitat's suitability and temperature (in B), highlighting the current and future ranges for (C) stronger vs. weaker dispersers; (D) the native vs. introduced range; (E) weak vs. strong interactors. For simplicity in the scenario for introduced species, we assume climate conservatism (i.e., no shift in the TPC with evolution following introduction) and limited dispersal in the introduced range (i.e., the species has not been introduced to a broader range of habitats). Range maps represent suitable areas that may or may not be occupied. Uncertainty (not spatially explicit) is depicted using pink diagonal lines and can be compared across scenarios. Note the range maps on the left side of C–E are the same.

Testable hypotheses

Here, we discuss hypotheses to help guide when the SFTS approach is likely to be predictive and how predictions are likely to be impacted when assumptions are less likely to be supported (i.e., if they are inaccurate and/or the degree of uncertainty is likely to increase [15–17].) We propose that the predictability of the SFTS approach will depend on species' traits, the ecological context, and if they are declining or introduced.

Traits

First, previous work has suggested that the time of generation and dispersal ability influence the predictability of the SFTS approach [18–20]. We expect that the SFTS approach will be more predictive for species with short(er) generation times and adequate or rapid dispersal because we are more likely to collect data (e.g., occurrences) that reflect the current climate's suitability. In contrast, current occurrence records for long-lived species (>30 years, defined according to the timescale of climate) could lag behind a changing climate, reflecting relic populations in locations where the climatic conditions are no longer suitable (e.g., 'legacy' effects related to the climate equilibrium assumption [21–23]), leading to overestimating the suitable future locations.

Species with adequate dispersal are more likely to reach all suitable habitats and thus not be missing from locations that are currently suitable, compared with dispersal-limited species (the climate equilibrium assumption [15,18,24,25]). Additionally, these species are more likely to move to new locations with suitable future conditions [26]. Comparatively, species with limited dispersal could be absent from suitable locations within or beyond the niche's limits [15,27]. Consequently, our predictions for species with limited dispersal could be overestimates if the species is likely to take longer than 30 years to reach all future locations (Box 1) or underestimates if the species is not currently at climate equilibrium.

Species with better dispersal are also more likely to have more genetic mixing among populations and fewer populations with local adaptation (i.e., the climate spatial conservatism assumption is less likely [28,29]). Consequently, preadapted genotypes are likely to be widely distributed if local genotypes become disfavoured by climate change. Conversely, species with better dispersal could make it more difficult for us to assess their adaptive potential and the level of climate spatial conservatism present in current populations (i.e., a methodological rather than biological challenge), thus leading to greater uncertainty in predictions. Local adaptation over space, however, can occur over a longer timescale than might be available as the climate changes. This could limit the degree of inferences we can make using dispersal ability to predict the future.

Ecological context

The predictability of the SFTS approach will also depend on ecological contexts such as the species' interaction strength and habitat specialization [26,30]. We expect that the SFTS approach will be more predictive for species with weak(er) interspecific interactions because they are more likely to have a stronger relationship with the climate (the climate determinism assumption) and more likely to be in all currently suitable locations (the climate equilibrium assumption [26,31,32]). Our predictions for species with strong interactions will have higher uncertainty, as they could both over- and/or underestimate the locations likely to be suitable in the future. These predictions depend on how multiple species respond to temperature, the type of interaction, and the role of each species in the interaction (Box 1). For example, the type of interaction could vary across the temperature gradient and degree of influence of a habitat's suitability. Strongly interacting alpine plants at high elevations (lower temperatures) could have higher suitability than expected on the basis of the physiological response alone (Box 1) given facilitation, whereas at low elevations (higher temperatures), the same species could have lower suitability than expected given competition [33].

In another example, if paired species in a facultative relationship track with suitable climates at different rates, then the strong interactor could lag at the poleward limit (e.g., facilitation stops occurring) and/or be slow to retreat from an unsuitable climate at the equatorial limit (e.g., if facilitation still occurs).

We hypothesize that the SFTS approach will be more predictive for species with more generalized than specialized habitat requirements (e.g., endemics or old-growth specialists). Habitat specialists are more likely to be limited by the availability of specific habitats than the climate itself (the climate determinism assumption [13]) and the habitat requirements will limit the suitable climate space otherwise available to them (the climate equilibrium assumption [26]). Predictions based on the current climate could be overestimates of the likely suitable future locations, depending on how the habitat also changes (e.g., if current models miss an important environmental constraint that does not correlate well with climate, such as the soil's properties [34]). Alternatively, we could be more likely to capture the entire realized niche of habitat specialists if the habitat itself is rare (the climate equilibrium assumption [4]), in which case, the SFTS approach has the potential to be predictive.

Declining and introduced species

Finally, we hypothesize that the predictability of the SFTS approach will depend on whether the species is anthropogenically rare (i.e., species that otherwise would not be rare [35]) or introduced. The SFTS approach will be less predictive for threatened species for three reasons. First, in human-dominated landscapes where threatened species are concentrated, landscape factors might influence the current distribution more than climatic factors (the climate determinism assumption [36]). Second, threatened species are less likely to be found in all locations with a suitable climate, given that their realized distribution has been anthropogenically contracted (the climate equilibrium assumption [36,37]). We note here that this prediction is contingent on (i) the reason(s) why the species is threatened, assuming that it is not climate change [26]; and (ii) the fact that not all historical processes and patterns are captured in current-day distributions. Third, threatened species also have a lower population frequency, making it more difficult to detect their presence, leading to extant populations that are unknown (the climate equilibrium assumption [36]).

For introduced species, we can make two opposing predictions, drawing solely on each range separately. First, the SFTS approach will be more predictive for the native range than the introduced range because introduced species, including recent introductions and/or those with rapid range expansion [38,39] have not yet had time to colonise all the suitable environments in the invaded range (the climate equilibrium assumption [40,41]). Typically, species only near equilibrium in the final stages of invasion [13,42]. Until then, forecasts are likely to underestimate the potential range of the species (Box 1) [43]. Alternatively, due to human-mediated and widespread introductions into suitable habitats, introduced species might not initially be limited in their dispersal. Since they have been able to colonise a larger portion of their potential range, they could be closer to climate equilibrium than native species [44].

A further complication of predictions for introduced species is the widespread debate about the prevalence of climate conservatism [45]. Niches can shift when species are introduced into new environments or due to new or increased selective pressures in the current environments. If niches are not conserved over time (e.g., if there is evolution in their environmental tolerance) or if populations are locally adapted (the climate spatial conservatism assumption), predictions are likely to have even greater uncertainty, particularly for short-generation species that are capable of rapid evolutionary change [22]. The degree and prevalence of niche shifts for introduced species remain a topic of recent debate [46,47].

Table 1. Select examples of studies that evaluate one of the assumptions underlying the space-for-time substitution (SFTS) hypothesis using observational approaches such as **climate matching**, **climate decoupling**, or spatial or temporal transferability. With this terminology, 'less accurate predictions' is similar in meaning to 'low transferability' and 'more decoupling'

Trait or context	Prediction	Study	Taxonomic group	Methodological approach ^a	Evidence	Support for hypothesis
Generation time	More accurate predictions for species with short(er) generation times	[5]	Breeding birds in North America	Spatial transferability with SDMs. Spatially blocked cross-validation: spatial data were withheld, then the model was tested on other regions of distribution	Short-lived species were more likely to have lower model transferability	No (opposite)
Dispersal	More accurate predictions for species with better dispersal	[54]	Vascular plants, birds, butterflies in Great Britain	Temporal transferability with SDMs. Compared current-day forecasts to current-day independent set of observations	Transferability was highest for butterflies, then plants, then birds	No
		[67]	Breeding birds in North America	(1) Spatial transferability using spatially blocked cross-validation. (2) Temporal transferability. Evaluated changes in climate matching at the same sites over 30 years	No relationship between climate decoupling and ability to disperse	No
		[4]	Vascular plants in California	Temporal transferability with SDMs. Compared forecasts and hindcasts with data from a different time period	Species with higher ability to disperse exhibited higher transferability than those with limited dispersal	Yes
		[26]	Breeding birds in North America	Climate matching: evaluated on the basis of predictive performance of species–climate models from abundance data	There was no relationship between the degree to which species showed climate matching and the hand–wing index (a proxy for the ability to disperse)	No
		[71]	Vascular plant species that are provincially rare in Canada	Spatial transferability using independent field surveys	Species with smaller seeds and species with animal- or wind-dispersed seeds had better modelled performance	Yes
		[72]	Multiple species (birds, butterflies, mammals, herptiles, and vascular plants), global	Climate matching; evaluated on the basis of the predictive performance of species–climate models from occurrence data	No relationship between modelled performance and dispersal distance	No
Habitat specialisation	More accurate predictions for species with more generalised habitat requirements than those with more specialised requirements	[26]	Breeding birds in North America	Climate matching: evaluated on the basis of the predictive performance of species–climate models from abundance data	Species that were more specialised were less well matched to the climate	Yes
		[67]	Breeding birds in North America	(1) Spatial transferability using spatially blocked cross-validation (2) Temporal transferability, evaluated as the change in climate matching at the same sites over 30 years	Habitat specialists became more decoupled from the climate relative to generalists	Yes
		[69]	Early winter ranges of resident and migratory birds in North America.	Temporal transferability with SDMs. Compared current-day forecasts with current-day models	Less transferable models for wide-ranging organisms with broad environmental niches than for narrow-ranging specialists	No
		[71]	Vascular plant species that are provincially rare in Canada	Spatial transferability using independent field surveys	No relationship between edaphic specialisation and modelled performance	No

Table 1. (continued)

Trait or context	Prediction	Study	Taxonomic group	Methodological approach ^a	Evidence	Support for hypothesis
Threatened status	More accurate predictions for species that are not threatened than for those that are	[26]	Breeding birds in North America	Climate matching: evaluated on the basis of the predictive performance of species–climate models from abundance data	Species classified as ‘near threatened’ were more well matched to the climate; species classified as ‘vulnerable’ were more decoupled from the climate than those of ‘least concern’	Mixed
Body size (correlated with generation time and ability to disperse)	More accurate predictions for bigger species, or small and large species	[26]	Breeding birds in North America	Used climate matching. Evaluated on the basis of the predictive performance of species–climate models using abundance	Climate matching was low for the smallest species, strongest for species with low to intermediate body mass, and decreased for the largest bird species (i.e., a quadratic effect)	Neither prediction
		[70]	Mixed, global extent	Used climate matching based on the area under the curve of a receiver operating characteristic plot from SDMs	Predictability showed a highly significant positive relationship with body size	Yes

^aRemove footnote for SDMs and include in table caption: SDM, species distribution models.

Moving forward

Comparative framework

To apply the SFTS hypothesis more effectively to anticipate future changes in biodiversity requires rigorous testing. We argue that the biological hypotheses we postulate here make testable predictions. To demonstrate the different sources of uncertainty and the types of bias that can arise using the SFTS approach, we advocate for a comparative approach across species that differ in a trait or context (Box 1). Given the inherent complexities and inaccuracies in forecasting species’ responses, our approach focuses on relative predictions (i.e., asserting the order of differences) rather than absolute predictions (i.e., specific values) that focus on accuracy [53]. For example, taxonomic groups with different dispersal abilities could be used to evaluate differences in **transferability** (Table 1).

While it is not a comprehensive list, the examples in Table 1 demonstrate mixed evidence for the role of these traits and contexts in determining when the SFTS approach is likely to be predictive. For example, there is evidence both for and against the prediction that models will be more accurate for species with better dispersal (Table 1). In part, this could be due to a lack of rigorously testing the underlying assumption of climate determinism before applying temporal transferability to these models (e.g., [54]). For the habitat specialization hypothesis, rigorous testing could be challenging because habitat and climate are not often independent. Nonetheless, these examples suggest a limited and taxonomically biased sample thus far and signal an opportunity to compare existing studies in a standardized framework (e.g., a meta-analysis) and to design new studies that explicitly make these comparisons (Box 1).

Testing hypotheses

Scientists and practitioners will still be required to make decisions regardless of whether the SFTS hypothesis is applicable or whether accurate predictions are even possible, given the uncertainty and complexity involved with forecasting (e.g., future climates will be outside the range of historical variability; see Outstanding questions). In some cases where the SFTS approach is less likely to be predictive (e.g., for long-lived species), adding biological and/or abiotic data with higher quality or more complex models (e.g., multispecies distribution models) could improve the

predictability (e.g., [48–50]). Given that the goal of SDMs is to quantify potential habitats' suitability, we suggest prioritizing further studies in cases of actual model error (underprediction; e.g., not occupying all their suitable habitat) rather than 'overprediction' (i.e., limited dispersal). Correctly identifying potentially suitable habitats could still be useful for assessing the risk of invasion or in planning assisted migration.

To resolve the challenge that range expansion could be ongoing for introduced species, recent work has argued that we should use the invasion history of the species and infer equilibrium when its distribution has remained stable in environmental space for an extended time [13]. Where predictions are required long before the necessary equilibrium is achieved [13], identifying outliers from relic populations, which are likely to generate uncertainty, could allow refinements of the predictions [51]. We also argue for estimations of shifts in niches and a consideration of nonanalogous climates between ranges to determine how to forecast the expansion of introduced species' ranges [47,52]. For example, if a substantial niche shift has occurred in the introduced range, the introduced range can be used to inform forecasts for that same continent.

To improve the predictability of the SFTS approach, we also join recent calls to integrate observational studies across an environmental gradient with transplant experiments with nonvertebrates to test assumptions of the SFTS hypothesis (e.g., [6,55,56]). For example, quantifying the prevalence of local adaptation could indicate the level of climate conservatism and, conversely, the potential for local adaptation over time [57]. Given the effort required for rigorous experiments and how poorly it has been studied in this context, we suggest prioritizing the climate determinism assumption, which is the most complex assumption to test, resulting in high uncertainty in our predictions (Box 1). For example, further testing how the relative importance of biotic interactions (e.g., the type and the asymmetry of strength) varies with latitude [58] or elevation [59,60] (e.g., by removing interacting species in both trailing and expanding ranges) would help determine whether and when the climate has a direct or indirect effect on fitness. This is a fundamental question that has challenged ecologists for centuries (e.g., [58,61]). An integrated approach could contribute to refining the relationship between a habitat's suitability and temperature (Box 1), which underlies the comparative framework.

Predicting where a species will be in the future is the first step in ensuring that the SFTS approach is predictive for anticipating species' responses to climate change. The next step, which is arguably even more challenging, is predicting how a species will perform in those locations. In the near-term, harnessing the SFTS approach to predict species' performance (i.e., growth and abundance) could still rely heavily on SDMs (e.g., [61]) but it is likely to increasingly leverage abundance data (e.g., [23,62]). This could be problematic, given their poor performance (e.g., [63,64]) and that the predicted habitat suitability has been shown to correlate poorly with metrics of a population's fitness (e.g., plant size or fitness [23]), albeit not always. In birds, density (correlated with high predicted suitability in SDMs) can be correlated with the quality of the habitat [65,66]. To forecast species' performance, higher-quality biotic data and alternative methods such as using demographic data or population modelling could be needed [67,68]. Assumptions that are even more critical to this next step of predicting species' performance (e.g., climate spatial conservatism [28,29]) will require more rigorous testing.

Concluding remarks

We urgently need to be able to anticipate where species will be in the future and, ultimately, how populations' abundances will change across species' ranges, particularly for declining and introduced species. Doing so requires us to confront the assumptions that are made when we use correlative approaches to make SFTSs. We argue that tackling this issue from two angles, namely

Outstanding questions

What are the most important sources of uncertainty that could arise using the SFTS approach? For example, for some species, the amount or extent of spatial uncertainty will be critical when guiding monitoring and management efforts.

How can we incorporate sources of uncertainty (e.g., outliers and relic populations) into our forecasts of species' geographic distributions?

When do the consequences of violations of the SFTS assumptions lead to biased predictions of geographic distributions in addition to increased uncertainty?

When is there likely to be decoupling (spatial and/or temporal) between the climate and other factors in determining occurrence?

When does performance not scale up well to the habitat's suitability and population growth?

What is a reasonable timescale at which the SFTS approach is likely to be reliable?

What is the best predictor of the strength of species' interactions across their geographic distributions?

Do species' traits predict the validity of the SFTS approach?

How well does spatial transferability in species–climate relationships predict the temporal transferability in species–climate relationships?

testing how violations of the assumptions of the SFTS hypothesis influence the uncertainty of our predictions, and refining SDMs by including additional data and/or taking different approaches when possible, will be key. In the absence of being able to validate forecasts, the importance of quantifying their uncertainty also increases. We see a comparative approach across species using a relative prediction framework as an important way forward to test the SFTS hypothesis and generate new predictions.

Acknowledgments

We are grateful to the editor and four anonymous reviews for their constructive feedback on this manuscript. We thank the University of British Columbia Department of Geography for providing office space for H.M.K. to work on this manuscript, and Amy Angert and Tyler Smith for their constructive feedback.

Declaration of interests

The authors have no interests to declare.

References

- Zografou, K. *et al.* (2020) Butterfly phenology in Mediterranean mountains using space-for-time substitution. *Ecol. Evol.* 10, 928–939
- Lester, R.E. *et al.* (2014) Predicting the likely response of data-poor ecosystems to climate change using space-for-time substitution across domains. *Glob. Chang. Biol.* 20, 3471–3481
- Viteri, M.C. and Hadly, E.A. (2022) Spatiotemporal impacts of the Anthropocene on small mammal communities, and the role of small biological preserves in maintaining biodiversity. *Front. Ecol. Evol.* 10, 916239
- Dobrowski, S.Z. *et al.* (2011) Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. *Ecol. Monogr.* 81, 241–257
- Rousseau, J.S. and Betts, M.G. (2022) Factors influencing transferability in species distribution models. *Ecography* 2022, e06060
- Lovell, R.S. *et al.* (2023) Space-for-time substitutions in climate change ecology and evolution. *Biol. Rev.* 98, 2243–2270
- De Lombaerde, E. *et al.* (2018) Responses of competitive understory species to spatial environmental gradients inaccurately explain temporal changes. *Basic Appl. Ecol.* 30, 52–64
- Jochner, S. *et al.* (2013) Can spatial data substitute temporal data in phenological modelling? A survey using birch flowering. *Tree Physiol.* 33, 1256–1268
- Guittar, J. *et al.* (2016) Can trait patterns along gradients predict plant community responses to climate change? *Ecology* 97, 2791–2801
- Klesse, S. *et al.* (2020) Continental-scale tree-ring-based projection of Douglas-fir growth: testing the limits of space-for-time substitution. *Glob. Chang. Biol.* 26, 5146–5163
- Blois, J.L. *et al.* (2013) Space can substitute for time in predicting climate-change effects on biodiversity. *P. Natl. Acad. Sci. U. S. A.* 110, 9374–9379
- Wogan, G.O. and Wang, I.J. (2018) The value of space-for-time substitution for studying fine-scale microevolutionary processes. *Ecography* 41, 1456–1468
- Foster, S.L. *et al.* (2022) Testing the assumption of environmental equilibrium in an invasive plant species over a 130 year history. *Ecography* 2022, e12933
- Damgaard, C. (2019) A critique of the space-for-time substitution practice in community ecology. *Trends Ecol. Evol.* 34, 416–421
- Pagel, J. *et al.* (2020) Mismatches between demographic niches and geographic distributions are strongest in poorly dispersed and highly persistent plant species. *P. Natl. Acad. Sci. U. S. A.* 117, 3663–3669
- Pagel, J. and Schurr, F.M. (2012) Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Glob. Ecol. Biogeogr.* 21, 293–304
- Zurell, D. *et al.* (2016) Benchmarking novel approaches for modelling species range dynamics. *Glob. Chang. Biol.* 22, 2651–2664
- Pulliam, H.R. (2000) On the relationship between niche and distribution. *Ecol. Lett.* 3, 349–361
- Thuiller, W. *et al.* (2004) Relating plant traits and species distributions along bioclimatic gradients for 88 *Leucadendron* taxa. *Ecology* 85, 1688–1699
- Porfírio, L.L. *et al.* (2014) Improving the use of species distribution models in conservation planning and management under climate change. *PLoS One* 9, e113749
- Foden, W. *et al.* (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Divers. Distrib.* 13, 645–653
- Wiens, J.A. *et al.* (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. *P. Natl. Acad. Sci. U. S. A.* 106, 19729–19736
- Lee-Yaw, J. *et al.* (2022) Species distribution models rarely predict the biology of real populations. *Ecography* 2022, e05877
- Soberón, J. and Nakamura, M. (2009) Niches and distributional areas: concepts, methods, and assumptions. *P. Natl. Acad. Sci. U. S. A.* 106, 19644–19650
- Schloss, C.A. *et al.* (2012) Dispersal will limit the ability of mammals to track climate change in the Western Hemisphere. *P. Natl. Acad. Sci. U. S. A.* 109, 8606–8611
- Viana, D.S. and Chase, J.M. (2022) Ecological traits underlying interspecific variation in climate matching of birds. *Glob. Ecol. Biogeogr.* 31, 1021–1034
- Hargreaves, A.L. *et al.* (2014) Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am. Nat.* 183, 157–173
- Angert, A.L. *et al.* (2011) Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integr. Comp. Biol.* 51, 733–750
- DeMarche, M.L. *et al.* (2018) Both life-history plasticity and local adaptation will shape range-wide responses to climate warming in the tundra plant *Silene acaulis*. *Glob. Chang. Biol.* 24, 1614–1625
- Wisz, M.S. *et al.* (2013) The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. *Biol. Rev.* 88, 15–30
- Gilman, S.E. *et al.* (2010) A framework for community interactions under climate change. *Trends Ecol. Evol.* 25, 325–331
- Abrego, N. *et al.* (2021) Accounting for species interactions is necessary for predicting how arctic arthropod communities respond to climate change. *Ecography* 44, 885–896
- Callaway, R.M. *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature* 417, 844–848
- Ni, M. and Vellend, M. (2021) Space-for-time inferences about range-edge dynamics of tree species can be influenced by sampling biases. *Glob. Chang. Biol.* 27, 2102–2112
- Raup, D.M. (1981) Extinction: bad genes or bad luck? *Acta Geol. Hisp.* 131, 25–33

36. McCune, J.L. (2016) Species distribution models predict rare species occurrences despite significant effects of landscape context. *J. Appl. Ecol.* 53, 1871–1879
37. Faury, S. and Araújo, M.B. (2018) Anthropogenic range contractions bias species climate change forecasts. *Nat. Clim. Chang.* 8, 252–256
38. Richardson, D.M. *et al.* (2000) Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6, 93–107
39. Pyšek, P. *et al.* (2020) Scientists' warning on invasive alien species. *Biol. Rev.* 95, 1511–1534
40. Elith, J. *et al.* (2010) The art of modelling range-shifting species. *Methods Ecol. Evol.* 1, 330–342
41. Gallien, L. *et al.* (2012) Invasive species distribution models – how violating the equilibrium assumption can create new insights. *Glob. Ecol. Biogeogr.* 21, 1126–1136
42. Václavík, T. and Meentemeyer, R.K. (2012) Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. *Divers. Distrib.* 18, 73–83
43. Elith, J. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography* 29, 129–151
44. Bradley, B.A. *et al.* (2015) Space to invade? Comparative range infilling and potential range of invasive and native plants. *Glob. Ecol. Biogeogr.* 24, 348–359
45. Liu, C. *et al.* (2020) Most invasive species largely conserve their climatic niche. *P. Natl. Acad. Sci. U. S. A.* 117, 23643–23651
46. Early, R. and Sax, D.F. (2014) Climatic niche shifts between species' native and naturalized ranges raise concern for ecological forecasts during invasions and climate change. *Glob. Ecol. Biogeogr.* 23, 1356–1365
47. Bates, O.K. and Bertelsmeier, C. (2021) Climatic niche shifts in introduced species. *Curr. Biol.* 31, R1252–R1266
48. Lany, N.K. *et al.* (2020) Complementary strengths of spatially-explicit and multi-species distribution models. *Ecography* 43, 456–466
49. Seaborn, T.J. *et al.* (2020) Integration of dispersal data into distribution modeling: what have we done and what have we learned? *Front. Biogeogr.* 12, e43130
50. Erickson, K.D. and Smith, A.B. (2023) Modeling the rarest of the rare: a comparison between multi-species distribution models, ensembles of small models, and single-species models at extremely low sample sizes. *Ecography* 2023, E06500
51. Barbet-Massin, M. *et al.* (2018) Can species distribution models really predict the expansion of invasive species? *PLoS One* 13, e0193085
52. Guisan, A. *et al.* (2014) Unifying niche shift studies: insights from biological invasions. *Trends Ecol. Evol.* 29, 260–269
53. Hendry, A.P. (2023) Prediction in ecology and evolution. *BioScience* 73, 785–799
54. Rapacciuolo, G. *et al.* (2012) Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. *PLoS One* 7, e40212
55. Bayly, M.J. and Angert, A.L. (2019) Niche models do not predict experimental demography but both suggest dispersal limitation across the northern range limit of the scarlet monkeyflower (*Erythranthe cardinalis*). *J. Biogeogr.* 46, 1316–1328
56. Greiser, C. *et al.* (2020) Climate limitation at the cold edge: contrasting perspectives from species distribution modelling and a transplant experiment. *Ecography* 43, 637–647
57. Bontrager, M. *et al.* (2021) Adaptation across geographic ranges is consistent with strong selection in marginal climates and legacies of range expansion. *Evolution* 75, 1316–1333
58. Paquette, A. and Hargreaves, A.L. (2021) Biotic interactions are more often important at species' warm versus cool range edges. *Ecol. Lett.* 24, 2427–2438
59. Brown, C.D. and Vellend, M. (2014) Non-climatic constraints on upper elevational plant range expansion under climate change. *P. Roy. Soc. B. Biol. Sci.* 281, 20141779
60. Alexander, J.M. *et al.* (2018) Lags in the response of mountain plant communities to climate change. *Glob. Chang. Biol.* 24, 563–579
61. Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or Preservation of Favoured Races in the Struggle for Life*, John Murray, London
62. Evans, A. *et al.* (2024) Shifting hotspots: climate change projected to drive contractions and expansions of invasive plant abundance ranges. *Divers. Distrib.* 30, 41–54
63. Huang, Q. *et al.* (2023) Modeled distribution shifts of North American birds over four decades based on suitable climate alone do not predict observed shifts. *Sci. Total Environ.* 857, 159603
64. Howard, C. *et al.* (2023) Local colonisations and extinctions of European birds are poorly explained by changes in climate suitability. *Nat. Commun.* 14, 4304
65. Bock, C.E. and Jones, Z.F. (2004) Avian habitat evaluation: should counting birds count? *Front. Ecol. Environ.* 2, 403–410
66. Haché, S. *et al.* (2013) Experimental evidence for an ideal free distribution in a breeding population of a territorial songbird. *Ecology* 94, 861–869
67. Viana, D.S. and Chase, J.M. (2022) Increasing climatic decoupling of bird abundances and distributions. *Nat. Ecol. Evol.* 6, 1299–1306
68. Ehrlén, J. and Morris, W.F. (2015) Predicting changes in the distribution and abundance of species under environmental change. *Ecol. Lett.* 18, 303–314
69. Wogan, G.O. (2016) Life history traits and niche instability impact accuracy and temporal transferability for historically calibrated distribution models of North American birds. *PLoS One* 11, e0151024
70. Soininen, J. and Luoto, M. (2014) Predictability in species distributions: a global analysis across organisms and ecosystems. *Glob. Ecol. Biogeogr.* 23, 1264–1274
71. McCune, J.L. *et al.* (2020) Do traits of plant species predict the efficacy of species distribution models for finding new occurrences? *Ecol. Evol.* 10, 5001–5014
72. Kharouba, H.M. *et al.* (2013) Do ecological differences between taxonomic groups influence the relationship between species' distributions and climate? A global meta-analysis using species distribution models. *Ecography* 36, 657–664